MATTER, LIFE, AND GENERATION

Eighteenth-century embryology and the Haller–Wolff debate

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Introduction: mechanism and embryology

In 1683, the French savant Bernard de Fontenelle offered the following rejoinder to the mechanical physiology of his day: "Do you say that beasts are machines just as watches are? Put a male dog-machine and a female dog-machine side by side, and eventually a third little machine will be the result, whereas two watches will lie side by side all their lives without ever producing a third watch" (1683:312). The ability of living organisms to recreate themselves is perhaps the most striking and most distinguishing feature of life. Not surprisingly, explaining the phenomenon of reproduction has remained a central issue in biology throughout the ages.

Fontenelle's comments were made just four years before the publication of Newton's *Principia*, at the height of the Scientific Revolution. The success of mechanical explanations in the physical and astronomical sciences led some investigators to apply this kind of reasoning to biology as well. Could life phenomena be explained on the basis of matter and motion? Were living organisms simply highly organized machines? Locomotion, sensation, the circulation of blood, the movement of fluids in plants, digestion, respiration – all were subjected to mechanical analysis. Reproductive phenomena were no exception, although the application of mechanism proved more problematic here.

In the late seventeenth and early eighteenth centuries, two rival schools of thought on the subject of generation existed. The preformationists believed that the embryo preexists in some form in either the maternal egg or the male spermatozoon.[1] Most also thought that all embryos had been formed by God at the Creation and encased within one another to await their future appointed time of development. Epigenesists, on the other hand, argued that each embryo is newly produced through gradual development from unorganized material. Various explanations were proposed for how this gradual formation is accomplished, yet epigenesists were united in their opposition to preexistence.

Although clashes occurred between preformationists and epigenesists throughout the Enlightenment, perhaps the most important of these was the debate that took place between Albrecht von Haller (1708–77) and Caspar Friedrich Wolff (1734–94). Haller, a renowned scientific figure, announced his support for preformation in 1758, just one year prior to the publication of Wolff's doctoral dissertation, which strongly endorsed epigenesis. The ensuing controversy, lasting for over a decade, crystallized many of the key issues of eighteenth-century embryology. The role of mechanism in biological explanation, the relationship of God to his Creation, the question of spontaneous generation, and the problems of regeneration, hybrids, and monstrous births – all these were points of issue in the Haller–Wolff debate.

More importantly, the controversy between Haller and Wolff illustrates the fundamental tie between biological and philosophical questions that existed in the Enlightenment period. Philosophical concerns were in fact largely responsible for the rise and popularity of preformationist theories over epigenesis. The clash between Haller and Wolff epitomizes this philosophical nature of eighteenth-century embryology, for Haller and Wolff came from widely divergent philosophical backgrounds. Haller, a Newtonian mechanist and a deeply religious man, held beliefs about the nature of the world and about scientific explanation that differed fundamentally from those of Wolff, whose own viewpoint derived largely from the tradition of German rationalism. Their debate over embryological development can be fully understood only when viewed as a controversy over these underlying philosophical differences. Furthermore, as representatives of two major Enlightenment schools of thought, Haller and Wolff illustrate two important cases of the ways in which philosophical issues guided much of eighteenth-century embryology. As such, an analysis of their work and their controversy sheds light on a number of aspects of biological thought during this period.

THE RISE OF PREFORMATION THEORIES

Although there were those who, before the late seventeenth century, believed that the embryo was in some fashion preformed in the body of the parent before conception, the notion that all embryos had existed from the beginning of the world was first formulated in the 1670s with the work of Malebranche, Swammerdam, Perrault, and others. These theories of preexistence, based for the most part on the concept of *emboîtement* (encasement), did not grow directly out of the earlier preformationist positions (see note 1). Rather, they arose in response to a set of difficulties and concerns that were prompted by the appearance in the mid-seventeenth century of several epigenetic theories of development, propounded by Harvey, Descartes, Highmore, Borelli, and others.

Both Aristotle and Galen had proposed theories of epigenesis, albeit with important differences between their two systems[2]; and it is largely within the context of Renaissance scholasticism, the heir to these two great thinkers, that William Harvey's *Exercitationes de generatione animalium* (1651) must be understood. Written largely as a commentary on the theories of Aristotle and Fabricius ab Aquapendente, Harvey's work was based on observations that he had made on deer and on incubated chicken eggs. Harvey combated the Galenic and Hippocratic two-semen theory then in vogue by claiming that he could find no female semen and by showing that in female deer dissected shortly after copulation there was no evidence of male semen entering the uterus. Consequently, the embryo could not be the result of the mixing together of male and female seminal material. Furthermore, through his famous dictum "Omne vivum ex ovo," Harvey proposed that all organisms, viviparous as well as oviparous, develop from a primordial egg. Not a preexisting germ, the egg was thought by Harvey to be a product of conception. Finally, Harvey's detailed observations of day-by-day development of chick embryos led him to conclude "that the generation of the chick from the egg is the result of epigenesis . . . and that all its parts are not fashioned simultaneously, but emerge in their due succession and order" (1651, 1847 trans.: 336).[3]

Although Harvey's work provided significant improvements over the theories of his predecessors, his views had limited success, partly because, by 1651, his Aristotelian mode of argumentation had begun to seem out of date. Contemporaneous with Harvey, however, was another promulgator of epigenetic development, René Descartes, who was the first to offer an explanation for generation based solely on matter and motion. Descartes dealt with animal physiology in his *Traité de l'homme*, the second part of his *Monde*, which was written in the 1630s but suppressed by Descartes because of its Copernican viewpoint. (Galileo had recently been condemned for like views by the Catholic church.) Published after his death, Descartes's *Traité de l'homme* proposed mechanical explanations for the phenomena of sensation, muscular movement, digestion, the circulation of the blood, and other vital functions.[4] Yet generation was left untreated, for Descartes remarked in a letter to Mersenne that he had given up trying to deal with this subject in his treatise (Descartes 1964–74, 1:254). In the late 1640s, when Descartes returned again to generation, he described this earlier stage in his thinking about the animal organism, noting "I had almost lost hope of finding the causes of its formation." Yet, he proclaimed in this same letter, "in meditating thereupon, I have discovered so much new land, that I hardly doubt that I can complete the whole of the Physics according to my desire" (5:261). Descartes saw the generation of animals as the last segment to come under the wing of his mechanical philosophy, forming there the completion of Cartesian physiology.

The result of Descartes's deliberations in the late 1640s was a small treatise *De la formation de l'animal*, published posthumously along with the *Traité de l'homme* in 1664. Here Descartes proposed an explanation for development based entirely upon the movement of particles. According to Descartes's system, reproduction begins with the mixing of semen from the male and female, resulting in a fermentation of particles. The movement of these particles leads to the formation of the heart, followed by the other embryonic parts. "If one knew what all the parts of the semen of a certain species of animal are, in particular, for example, of man," Descartes declared, "one could deduce from this alone, by reasons entirely mathematical and certain, the whole figure and conformation of each of its members" (1664: 146). Through matter and motion alone, one can explain not only the inanimate but the animate world as well. "It is no less natural for a clock, made of a certain number of wheels, to indicate the hours," he proclaimed, "than for a tree born from a certain seed, to produce a particular fruit" (1644:326).

Descartes's explanation for embryological development by mechanical causation was not a successful one. In particular, it failed, as did those of other mechanistic epigenesists, to explain *why* development proceeds as it does, that is, why the proper organism, with its parts perfectly arranged, is formed. How does a process based on matter and motion alone result in a complex living organism?

This insufficiency of mechanical explanations of gradual development was an important element in the rise of preexistence theories. As Nicolas Malebranche noted in 1688 concerning Descartes's theory of epigenesis, "The rough sketch given by this philosopher may help us understand how the laws of motion are sufficient to bring about the gradual growth of the parts of the animal. But that these laws could form them and link them together is something that no one will ever prove" (1688:264). It does not seem possible that mechanical laws could both fashion and organize the parts of the organism. "It is easy to see," Malebranche declared, "that the general laws of the communication of motion are too simple for the construction of organic bodies" (p. 252). Mechanical causes may be part of the process of development, but they cannot account for reproduction itself.

Malebranche was the first to fully articulate, in 1674, a theory of preformation by *emboîtement.* In discussing the limits of our senses, especially vision, Malebranche turned to biological examples. If one looks closely at a tulip bulb, using a magnifying lens, one can see all the parts of the future tulip folded up in miniature inside the bulb. And one can assume that the same may be the case in the seeds of all trees and plants. "It does not even seem unreasonable," Malebranche declared, "to think that there are infinite trees in a single germ, since it does not contain only the tree which is the seed, but also a very great number of other seeds, which are all enclosed in those of the new tree. . . . one can say that in a single apple pit, there would be apple trees, apples, and the seeds of apples for infinite or almost infinite centuries" (1674:82). Each seed, then, would contain the seeds of all future individuals, encased within one another. This notion can be extended to cover animals as well: "One sees in the germ of the bulb of a tulip the entire tulip. One sees also in the germ of a fresh egg, and which has not been covered, a chicken which is perhaps entirely formed. One sees frogs in the eggs of frogs, and one will see other animals in their germs, when one has appealed to and experimented enough to discover them" (pp. 82-83). From all of this evidence we can conclude, according to Malebranche, "that all the bodies of men and of animals, which have been born up to the consummation of the century, have perhaps been produced as long ago as the creation of the world" (p. 83; see also Schrecker 1938).

In his discussion of animal *emboîtement,* Malebranche referred to the work of Marcello Malpighi on chick eggs and of Jan

Swammerdam on frogs. Malpighi had shown in his *Dissertatio epistolica de formatione pulli in ovo* (1673) that one can observe, in eggs that have been fertilized but not yet incubated, the rudiments of the embryo already formed. Although Malpighi never argued for the preexistence of embryos before fertilization (and in fact reported that one can see nothing in the unfertilized egg), his observations were quickly taken up, by Malebranche and others, as evidence for preformation. By the eighteenth century, Malpighi was regularly cited as a preformationist. That the rudiments of the chick embryo could be seen from the earliest moments became a principal example in support of the preexistence of all germs.[5]

Even more important, Malpighi contributed the first detailed series of observations on the development of chick embryos.[6] Before Malpighi, Aldrovandi, Coiter, Fabricius ab Aquapendente, Harvey, and others had based their work on observational investigations; yet Malpighi's careful hour-by-hour descriptions of developing embryos, accompanied by superb illustrations (see Figure 1), represented a major advance over prior attempts to understand embryological development. Many of Malpighi's drawings are so clear and so detailed that they stand up well even when compared with modern-day diagrams. Observation and description were Malpighi's forte, and his declining to elaborate a clear theoretical position in his treatises undoubtedly contributed to later confusion over his views on preformation.

In a similar way, Swammerdam's observations on frogs' eggs and on the development of insects were seen as providing important evidence for preformation. In his book on insects published in 1669, Swammerdam claimed that one could observe the structure of the butterfly folded up within the chrysalis, and the wings and other parts in the dissected caterpillar. Initially directed against the theory of metamorphosis advocated by Harvey and others (that the caterpillar becomes transformed all at once into the butterfly), Swammerdam's observations were used by preformationists as an example of development from preexisting parts. Similarly, Swammerdam's brief comments on frogs' eggs made in 1672, where he remarked that the black spot in the egg is "the frog itself complete in all its parts" (1672:21), were cited by Malebranche and others as further evidence in support of preexistence.

Although Swammerdam expressed support for the notion of *emboîtement* in brief passages in 1669 and 1672 (see Roger 1963:

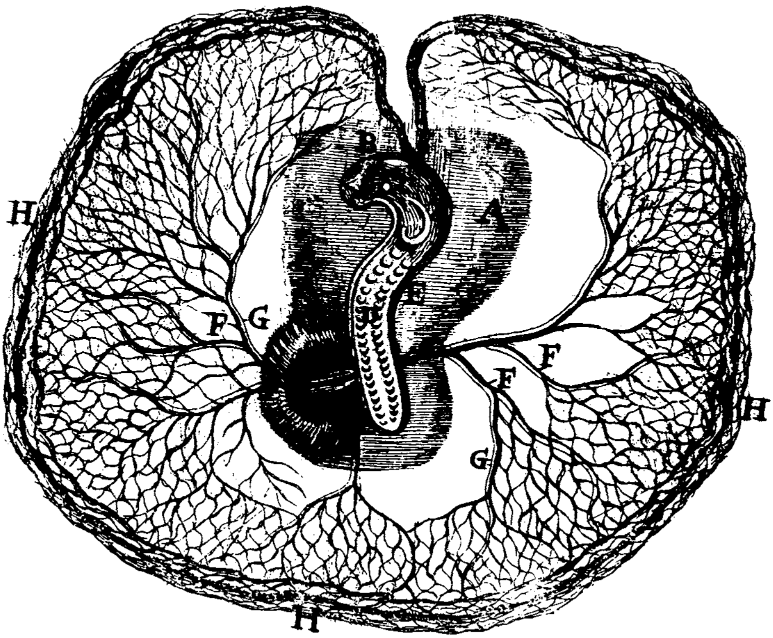

Figure 1. Malpighi's illustration of a chick embryo at 62 hours, showing the blood vessel network extending out over the yolk in the area vasculosa. (From *Opera omnia*, 1686; reproduced by permission of the Houghton Library, Harvard University)

334–35; Bowler 1971:238), his own principal concern was to combat the theories of insect metamorphosis and spontaneous generation. Yet the fact that his and Malpighi's observations were immediately taken up by those making preformationist claims indicates that the concept of preexistence was not one that grew out of observational evidence alone. It is clear, as several scholars have pointed out, that preformation through preexistence was a theory that responded more to philosophical than to observational needs.[7] As in the case of Malebranche, one of the principal motivations behind preformationist theories was the need to combat the implications that a fully mechanistic epigenetic position entailed. Although it was widely believed in the late seventeenth century that the universe must operate through mechanical laws, it was also felt that these laws were not sufficient to account for its origins and especially for the construction of living organisms. Claude Perrault, another early proponent of development through preexisting germs (although in his case through panspermism rather than encasement), made explicit his concern over the limits of mechanical laws. As he remarked in 1680, "I do not know if one can comprehend how a work of this quality would be the effect of the ordinary forces of nature. . . . for I find finally that it is scarcely more inconceivable . . . that the world has been able to form itself from matter out of chaos, than an ant can form another from the homogeneous substance of the semen from which it is believed to be engendered" (p. 481). For Perrault, a mechanical universe could not possibly be responsible on its own for the formation of living creatures. George Garden, an early supporter of animalculist preformation, claimed in a similar vein that "all the laws of Motion which are as yet discovered, can give but a very lame account of the forming of a Plant or Animal. We see how wretchedly Des Cartes came off when he began to apply them to this Subject; they are form'd by Laws yet unknown to Mankind, and it seems most probable that the *Stamina* of all the Plants and Animals that have been, or ever shall be in the World, have been formed *ab Origine Mundi* by the Almighty Creator within the first of each respective kind" (1691:476–77).

The rise of preformationist theories in the late seventeenth century was thus a response principally to a series of philosophical problems posed by the application of mechanical explanation to embryology. It was not only that mechanical epigenesis seemed incapable of accounting for why the embryo develops as it does, although this was an important problem. But even more significantly, it was the implications of a fully mechanistic embryology that were the most disturbing. If matter could form organized beings, living creatures, then what role was left for the Divine Creator? Preformation through *emboîtement* provided a solution to this difficulty while still preserving a mechanical universe. All organisms were formed by God at the Creation and encased within one another, so that at the appointed time each tiny preformed embryo could expand and develop, through mechanical means, into a full-fledged organism. Preexistence avoided the atheistic and materialistic implications of development by epigenesis, while also accounting for the source of animal organization. Embryos develop into the proper organisms because all of their parts were created at one time and arranged in the proper fashion by God.

The impossibility of mechanistic epigenesis was further enhanced by the identification, commonly made, between mechanism and blind chance. Matter was viewed by most as entirely passive, put into motion only through mechanical laws. But since these laws of motion are blind, that they could know how to form a living organism seemed out of the question. Both self-active matter and a God actively involved in each instance of generation were ruled out in the mechanistic universe of late-seventeenth-century thinkers. The theory of preformation offered the only account of embryological development consistent with this view of a divinely created, mechanically operating world.

By the beginning of the eighteenth century, the theory of preformation was widely accepted. Animalculism was adopted by some, notably Hartsoeker, Nicolas Andry, Boerhaave, and Leibniz; yet the notion of preexistent germs in the male spermatozoa never made the same headway that ovist preformation did. The principal difficulty lay in the tremendous waste that male *emboîtement* would imply. Why would God have created so many creatures in spermatozoa destined never to develop? Regnier de Graaf's work on the female reproductive organs, published in 1672, had established that mammals develop, like oviparous animals, from a female egg, although the actual mammalian ovum was not observed until the nineteenth century.[8] Ovist preformation theories were widely adopted in the early eighteenth century, prompting both new observational studies on egg development and continued support for *emboîtement*.

REGENERATION AND THE FRESHWATER POLYP

During the first half of the eighteenth century, regeneration became a subject of increasing study. Both Thévenot and Perrault had described regeneration in lizard tails in the 1680s, but the first major work in this area was Réaumur's memoir on the regeneration of crayfish claws that appeared in 1712 (see Moeschlin-Krieg 1953; Roger 1963:390–96). Réaumur drew the parallel between regeneration and normal generation and was critical of the notion that hidden "germs" might be responsible for the development of the new appendages. Yet, Réaumur noted, all other hypotheses seemed inconceivable as well (Roger 1963:392–94).

The most astonishing development in this area came with Abraham Trembley's discovery in 1741 of a new animal, the freshwater polyp. Trembley, who observed the common green hydra, initially assumed the organism was a plant. Yet the creature's ability to contract when stimulated and to "walk" by attaching successively its posterior and anterior ends to the surface of an object raised doubts in his mind. Trembley then proceeded to cut a polyp in two, assuming that the two halves might live if it was a plant. "However," he admitted, ". . . I expected to see the cut polyps die" (1744:26). To his surprise, not only did both halves live, but each grew into a new complete animal. As Réaumur, to whom Trembley communicated his findings, expressed this sentiment, "when I saw for the first time two polyps form little by little from the one that I had cut in two, I could hardly believe my eyes; and it is a fact that I am not accustomed to seeing after having seen it again and again hundreds and hundreds of times" (1734–42, 6:liv–lv). Trembley also observed the polyp's normal reproductive method, that is, by budding, a further indication of the plantlike properties of this unusual animal (see Figure 2; see also Baker 1952).

Trembley's discovery of the polyp's ability to multiply *par boutures*, by artificial division, created a tremendous stir among eighteenth-century intellectuals. Réaumur, who announced Trembley's findings and demonstrated his experiments before the Paris Academy of Sciences in 1741, remarked, "I have seen no one who has believed this on the first account he has heard of it" (1734–42, 6:li). The official report of these sessions captures some of the excitement and sense of wonder that must have been present:

> The story of the Phoenix that is reborn from its ashes, wholly fabulous as it is, offers nothing more marvelous than the discovery of which we are about to speak. The chimerical ideas of the palingenesis or regeneration of plants and animals, which some alchemists have thought possible by the assembly and reunion of their essential parts, only tended to restore a plant or an animal after its destruction; the serpent cut in two and said to join together again, only gave one and the same serpent; but here is nature going farther than our fancies. [*Histoire de l'Académie Royale des Sciences*, 1744:33–34]

What was it about the polyp's unusual regenerative capabilities that was so astonishing and so disturbing? The Paris report concludes by recommending that the reader "draw his own consequences" from the polyp's behavior "on the generation of animals, on their extreme resemblance with plants, and per-

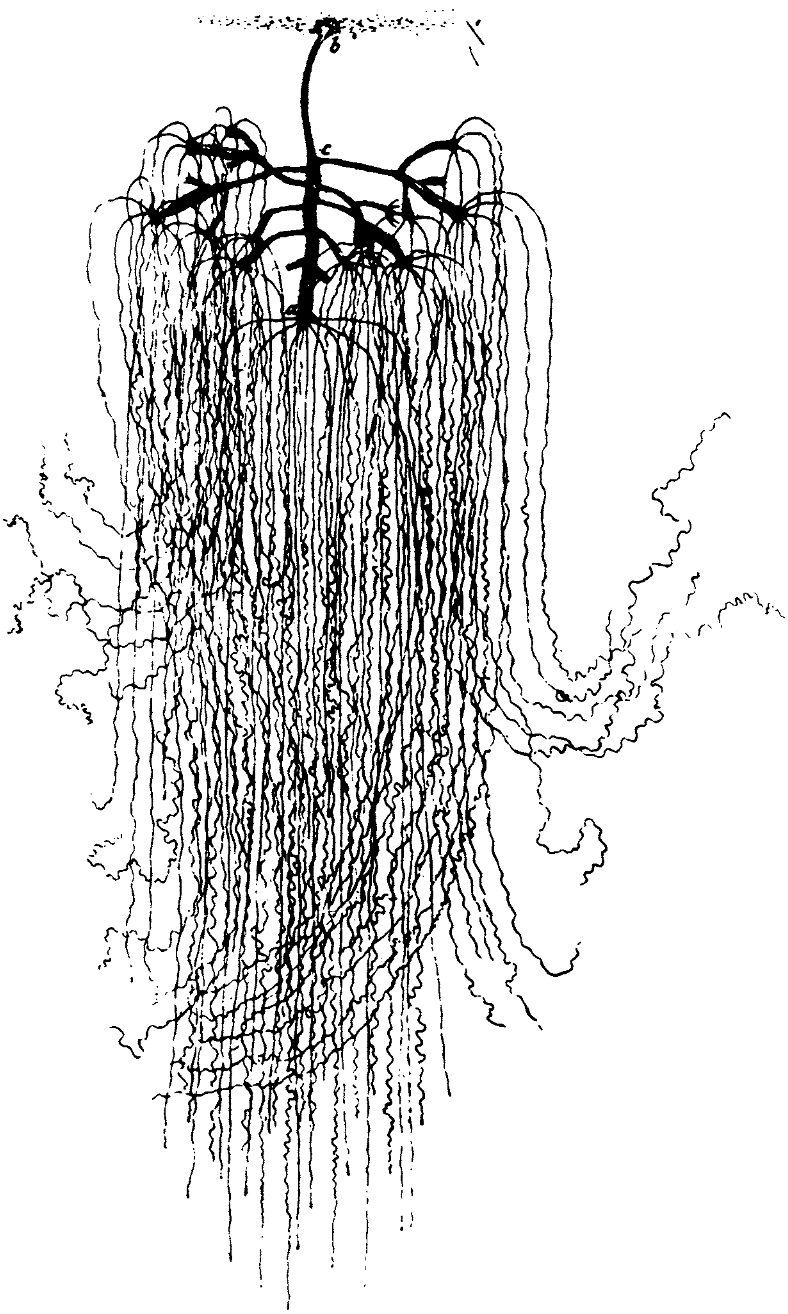

Figure 2. Trembley's illustration of polyps reproducing by budding. (From *Mémoires pour servir à l'histoire d'un genre de polypes d'eau douce,* 1744; courtesy of Cornell University Library)

haps on even higher matters" (1744:35). The polyp's ability to multiply by artificial division raised important questions concerning the divisibility of the soul (Were two new polyp-souls created with two new heads?), the continuity or discontinuity between the plant and animal kingdoms (Was the polyp the intermediate link?), and the nature of animal generation (What implications did regeneration in the polyp hold for normal generation?). At a time when most naturalists believed in preordained generation through the encasement of embryos, the polyp's capacity to create whole new organisms from small pieces of a former polyp was a most unexpected phenomenon. As Aram Vartanian has remarked, "In the pieces of a cut-up polyp regenerating into complete new polyps, Trembley's contemporaries had the startling spectacle of Nature caught, as it were, *in flagrante* with the creation of life out of its own substance without prior design" (1953:388).

Some naturalists responded by proposing that all regeneration is a product of preformed germs contained within the bodies of polyps and other organisms that are destined to develop if an accident occurs. Others saw in the polyp unmistakable evidence for epigenesis. Finally, there were those who simply refused to acknowledge the facts. As Trembley noted, in describing the reaction of the Royal Society to his discoveries, "The singular facts that are contained in the history of these small animals are the admiration of a great many people: but several people have been hesitant to admit them. There are those who have even said that they will not believe it when they see them. Apparently these men have some cherished system that they are afraid of upsetting" (M. Trembley 1943:165–66).

The episode of the polyp illustrates well the close dependence of eighteenth-century theories of generation on philosophical, metaphysical, and religious issues. The polyp was instrumental in the conversion of some to epigenesis (Bodemer 1964), and became a central motif in the materialist theories of epigenesis propounded by Diderot and La Mettrie (see Vartanian 1950). Yet after creating such an initial stir, regeneration in the polyp and in other organisms was quickly subsumed by preformationists like Charles Bonnet under ad hoc explanations based on preexistent part germs. As Roger has noted, it would seem "as if this system . . . was more valuable than the facts themselves" (1963:385).

EPIGENESIS AND ATTRACTION

Maupertuis

Prior to the mid-eighteenth century, the theories of epigenesis that preformationists sought to combat were based for the most part on mechanistic models of particle movement and fermentation. Yet in 1745, when the anonymously published *Vénus physique* appeared, a new challenge to preformationism arose – epigenesis through attractive forces. As Maupertuis, the author of this small treatise, explained, "The Astronomers were the first to feel the need of a new principle to explain the movements of the celestial bodies and thought they had discovered it in these very movements. Since then chemistry has felt the same necessity of adopting this concept, and the most famous Chemists admit Attraction and extend its function farther than had been done by the Astronomers. Why should not a cohesive force, if it exists in Nature, have a role in the formation of animal bodies?" (1745, 1966 trans.:55–56).

Maupertuis proposed that the seminal fluid in both the male and female parents contains particles sent from each part of the body. When these two fluids mix, the proper embryo results by a union of the particles from each part of the parents' bodies. "If there are, in each of the seminal seeds," Maupertuis explained, "particles predetermined to form the heart, the head, the entrails, the arms and the legs, if these particular particles had a special attraction for those which are to be their immediate neighbors in the animal body, this would lead to the formation of the fetus" (p. 56). As an analogy for this formation of the embryo by attractive particles, Maupertuis suggested the *arbre de Diane*, a treelike figure that forms on the surface of water from the mixture of silver, nitric acid, and mercury. Other similar examples of "organized" nonliving formations were known to be abundant in chemical phenomena. Why may these not serve as examples of the way embryos form? "Although these seem less highly organized than the bodies of most animals, might they not depend on the same mechanisms and on similar laws?" Maupertuis asked (p. 55).

Maupertuis opposed preformation on the grounds that it is no easier to explain how all organisms were formed at one time in the past than at each new instance of generation. "What has